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PROCEEDINGS OF THE
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Volume 16. 1941.

THE HEAD OF *SCATOPHILA UNICORNIS* CZERNY (DIPTERA)

By Niels Bolwig, M.Sc., F.R.E.S.

When redescribing *Scatophila unicornis* Czerny (Ephydridae, Diptera) I found that many of the structures of the head were so easy to see that it seemed worth while to study them a little more closely. This was confirmed by discovering that relatively few investigations have been carried out on this subject. The study was carried out by simple dissection under a microscope, or by examination of the whole head under a binocular, or monocular, microscope. The head of a newly hatched fly is the best subject. All the diagrams were made by the help of Bolwig's drawing apparatus. I am indebted to Statens Plantepatologiske Forsøg for being allowed to carry out my studies there and to the chief of the Zoological department of the laboratory, Dr. P. Bovien.

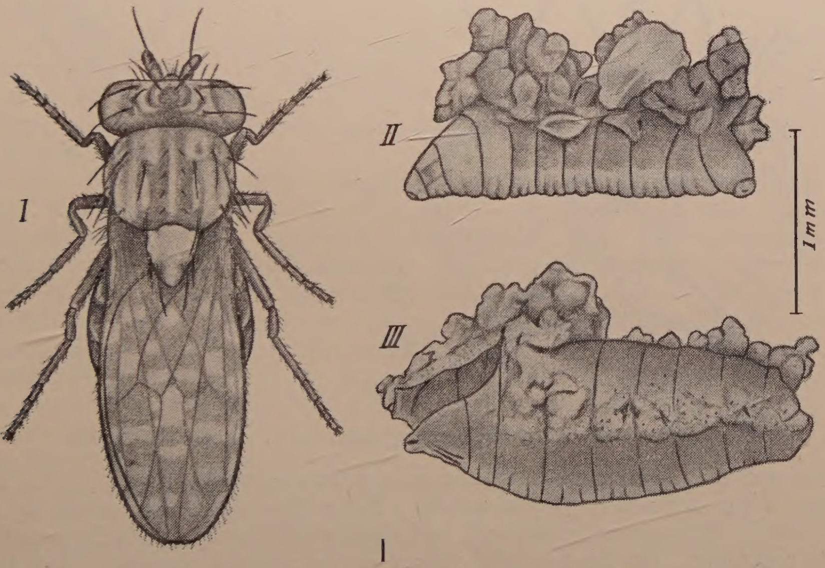


Fig. 1.—*S. unicornis,* I. Imago, II. Larva, III, Puparium.

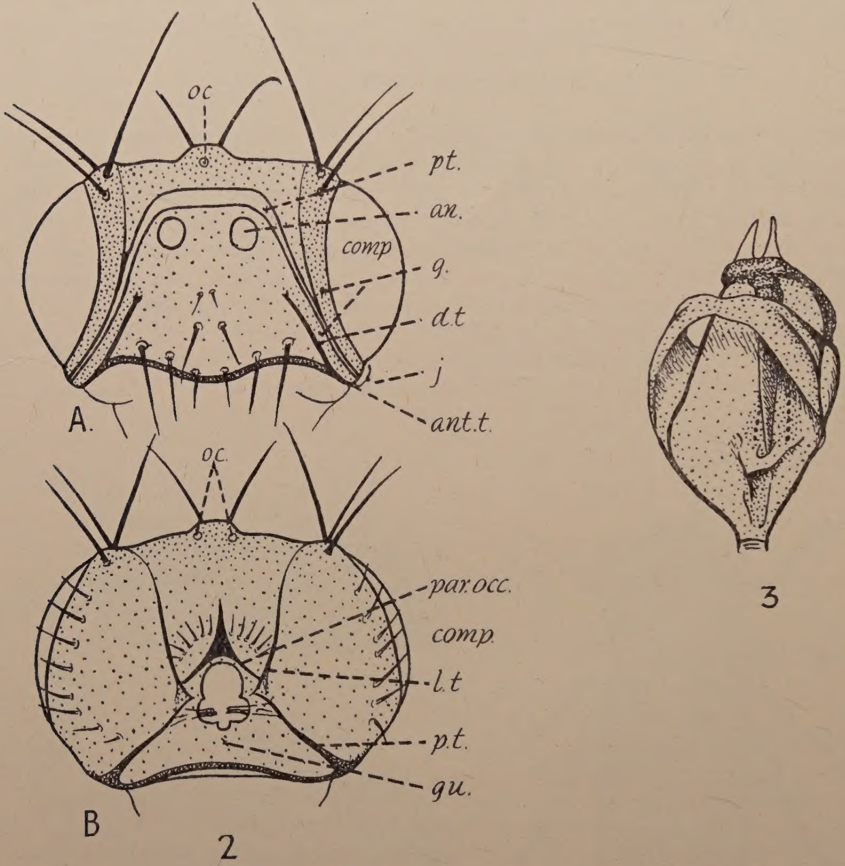
The Head Capsule.

The hypothetical head capsule of a fly has on each side a pair of large compound eyes. An *occipital foramen* is situated on its posterior aspect; another, very large orifice, the *mouth opening,* is situated in its lower side.

From the occipital foramen extends a suture over the dorsal side of the head passing down over the anterior surface of the head where it forks. Each of the arms continues down towards the mouth opening. This suture is named the *epicranial suture.*

On each side of the upper branch of the epicranial suture, just above the place where it branches, the *antennae* are situated.

The area between the two arms of the epicranial suture is named the *frons* (Peterson) (= the *praefrons*, de Meijere, 1915). The part of the head above the arms of the suture is named the *vertex* (Peterson). The antennae are situated in the vertex. Above the antennae is a suture formed like an "n". This suture is the *ptilinal* or *frontal suture.* From this place, the young fly can push out the *ptilinum* or *frontal sack,* by help of which the fly bursts the puparium when emerging. On the top of the head is seen a small plate on which three small *ocelli* are seen, the one in front of the others. The area of the vertex near the compound eyes is called the *temple.* Downwards between the eyes and the ptilinal suture, the vertex continues in the *genae* (Peterson). These again continue in the *jowls* (= *genae,* Peterson), the part of the head between the eyes and the mouth opening. The antennae are often situated in grooves. These grooves are the *antennal grooves.* They extend from the base of the antennae to the mouth opening.



Figs. 2–3.—2. *S. unicornis,* head capsule; 3. *S. unicornis,* fulcrum.

" No sutures occur on the caudal aspect of the hypothetical head-capsule, except the epicranial suture. This absence of sutures makes it impossible to locate definitely the boundaries of the occiput and the postgenae " (Peterson, 1916 : 23). The area dorsal of an imaginary line drawn through the middle of the occipital foramen is called the *occiput* (Peterson, 1916 : 23). The area ventro-laterally of this line has been called the *postgenae* by Peterson. The area just beneath the occipital foramen is named the *gula* by most authors. Peterson supposed that this area is made by fusion of the median borders of the postgenae.

The head of most insects has an inner skeleton, the *tentorium*, formed by three pairs of invaginations. These invaginations are seen as impressions of the head capsule. The one pair of impressions is seen just below the antennae, in the arms of the epicranial suture. From this point a pair of slender arms extend downwards and backwards into the cavity of the head capsule. These arms are the *dorsal arms* of the tentorium. In their distal end they fuse with another pair of arms : the *anterior arms* of the tentorium. They extend backwards from another pair of impressions in the epicranial suture just above the mouth opening. In the middle of the head the anterior arms meet and fuse with the *posterior arms* that point forwards from a pair of impressions just below the occipital foramen.

The dorsal half of the occipital foramen is strengthened by a thickening of the lower edge of the occiput. This thickening is named the *paraocciput* by Peterson. It is provided on each side with an articulation to the *cervical sclerites*. Below the occipital foramen is another thickening, the *parapostgenial thickening* (Peterson). The posterior arms of the tentorium arise from this thickening.

The head capsule of *Scatophila unicornis* (fig. 2) is strongly pigmented. Its colour is dark brown. In most parts of the head the true colour cannot be seen because of fine structures in its surface that give it a whitish, powdery appearance. Some places appear more powdery than others which show certain definite ornaments.

The head capsule is broader than high. Its anterior aspect is convex. The back of the head is flattened. The mouth opening is very wide. The *genae* (g) and *jowls* (j) are very short. The *ptilinal suture* (pt. s.) stretches nearly all the way to the mouth opening. Just as in most Diptera, there is no *epicranial suture* present on the vertex. Below the antennae is seen a pair of small invaginations. From these invaginations a pair of chitinous thickenings extend (d.t.) downwards to the mouth opening. Here they join another thickening, following the mouth opening all the way round. From the occipital foramen another pair of thickenings (p.t.) extend downwards and fuse with the thickening that surrounds the mouth opening. The triangular plate between the occipital foramen, the mouth opening and the thickenings that extend from the occipital foramen to the mouth opening, is the *gula* (gu). Most authors agree that the above-mentioned thickenings are the tentorium laid up to the head capsule and fused with it. Meanwhile there is some disagreement in explaining the homology of the thickenings. Most authors are of opinion that those extending from the impression beneath the antennae to the mouth opening (d.t.) are homologous with the *dorsal arms* of the tentorium. The lateral thickenings (ant. t.) of the edge of the mouth opening are then supposed to be homologous with the *anterior arms* of the tentorium, while the thickenings stretching from the occipital foramen downwards (p.t.) to the mouth opening are supposed to be homologous with the *posterior arms* of the tentorium. Against this point of view is that of Frew (1923). He has found that the thickenings of the anterior surface of the head of *Chlorops* extend, not from a point below the antennae, but from a point between the antennae from which the thickenings go upwards and outwards, round the base of the antennae, so that the antennae are placed between the thickenings instead of outside and above them. This means that if the antennae are considered to be the dorsal arms of the tentorium, marking the lower arms of the epicranial suture, it would be necessary to consider the area in which the antennae are situated as the frons. Such a position of the antennae is not known in insects. Therefore Frew concluded that the thickenings, extending from the antennae to the mouth opening, cannot be homologous to the dorsal arms of the tentorium. He tried to find the dorsal arms somewhere else. Peterson said in his description of *Tabanus* (1916 : 28) that " the invaginations of the lateral half of the head are joined together by the arms of the epicranial suture." Frew saw a similar connection in the thickening of the anterior margin of the mouth opening, which means that he considered the whole anterior surface of the head as the vertex.

I cannot say whether Frew is right or not, but the depression at the upper end of the thickenings below the antennae seems to prove that the ridges of *Scatophila* and at least the lower end of the ridges of *Chlorops* are homologous with the dorsal arms of the tentorium. Therefore, I think it right, until something more definite is known, to consider the thickenings below the antennae in *Scatophila* as homologous with the dorsal arms of the tentorium and the area between them to be the frons (Peterson).

The antennae are situated in the upper end of a pair of very low impressions. These impressions are the *antennal grooves*. In the males, the front is drawn out in a little " nose " just above the mouth opening (fig. 1).

Besides the tentorial thickenings of the rear head there is a thickening above the occipital foramen, this is the *paraocciput* (Peterson). Its middle is drawn out in a thickening that stretches upwards towards the ocelli. Laterally it joins a pair of thickenings (l. th.) which stretch towards the upper end of the compound eyes.

THE ANTENNAE.

The *antennae* are composed of three segments. They are inserted in the middle of the anterior aspect of the head capsule in the upper end of the antennal grooves. The first segment is formed like a little cone which is inserted into the head capsule with its top. The second is conical also, but a little compressed from side to side; its distal end is surrounded by an edge on which are situated a row of dark bristles pointing forwards. The third segment is nearly as long as the first two together and is strongly compressed from side to side. In side view it is almost ovoid and inserted into the second segment with its broadest end. Its surface is covered with little hairs. On its dorsal side, near its base, is inserted a long, bent, black, pubescent bristle pointing forwards. This bristle is the so-called *arista*. The arista is not a true bristle, but the rudiment of the distal end of the antennae. That it is so is proved by a little chitinous ring that separates the main part of the arista from the third segment of the antennae.

THE PROBOSCIS.

The proboscis consists of three parts, named respectively from above downwards : the *basiproboscis* or the *rostrum* (rost.); the *medioproboscis* or *haustellum* (haust.); and the *distiproboscis*, *oral disc* or *oral sucker* (or. d.). When at rest, the parts are flexed on each other, but the proboscis, because of its great size, can only be partly withdrawn within the head capsule. When fully extended, it projects downwards, the three parts being nearly in a straight line. When extended, it forms a broad inverted cone. The extension is, according to Lowne (1890–92), brought about by distention of large air-sacks which are contained within it. The retraction and the varied movements of the proboscis are produced by muscular action. For the most part it is covered by a thin membranous wall, but this wall is in some places interrupted by thicker chitinous sclerites to which muscles are attached.

THE SKELETON.

The *rostrum* (rost.) is the basal part of the proboscis. Its wall is a thin flexible membrane that is attached proximally to the margin of the epistomal orifice in front of the head capsule. These margins are formed in front by the *facial plate,* laterally by the *genae* and posteriorly by the *postgenae.* At its distal end, the wall of the rostrum is continued with that of the *haustellum* (haust.). In the anterior or dorsal surface of the rostrum is a dark horseshoe-shaped sclerite, the anterior arch of the internally-placed *fulcrum.* Lowne (1890–92) and Graham-Smith (1930) describe a little plate between the anterior arch of the fulcrum and the margin of the facial plate (the *epistome*) in the blow-fly. In *Scatophila unicornis* there is no such plate. Below the visible part of the fulcrum there lie on either side of the middle line the clavate *maxillary palps.* As in the blow-fly, no *palpigerous scale* is developed. The palpi articulate directly in the membranous skin of the rostrum. They are reddish-brown, pubescent and, near their end, carry two small dark hairs. In the blow-fly, a little *sesamoid sclerite* is seen at each side of the proboscis near its distal end to which are attached muscles. There are no such sclerites in *Scatophila unicornis.*

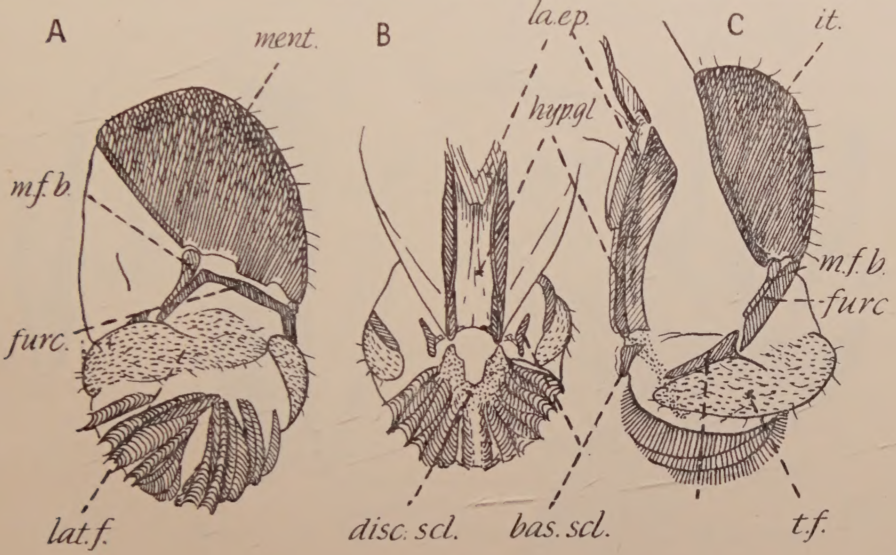


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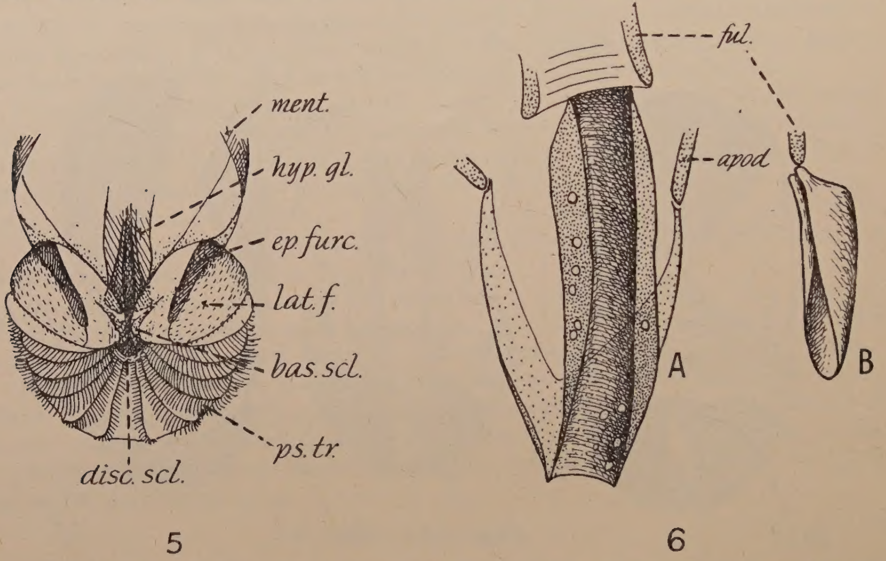
FIG. 4.—*S. unicornis,* the haustellum and the oral disc seen in A, nearly ventral aspect, B, from the dorsal side (the hypoglossa, hyp. gl., is pressed open by the covering glass) and C, from the left side.

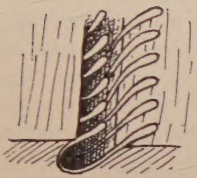
The most important structure of the rostrum is the *fulcrum* (fig. 3). The fulcrum is in the form of a stirrup, the visible part being at the top of the bow. The rest of the fulcrum is situated inside the rostrum. The sides of the arch form the *lateral plates*. The sole of the stirrup is large and oval and has its longest axis extended in the same direction as the main axis of the rostrum. In its upper end, the sole bends forwards towards the facial plate. From the edge of the upper end of the sole a pair of small *cornua* project upwards and backwards towards the vertex. Another pair of cornua project downwards from the lower end of the fulcrum. The sole and the lateral plates of the stirrup are double-walled. The sole consists of an outer ventral plate (fig. 8), the *hypopharyngeal plate* (hyp. ph. pl.) and an inner *epipharyngeal plate* (ep. ph. pl.). The hypopharyngeal plate is firmly connected to the lateral plates, while the epipharyngeal plate is connected to the lateral plates by a thin sheet of chitin that passes from the edge of the lateral plates. The cornua are situated on the hypopharyngeal plate. The *pharynx* is situated in the cavity between the two walls of the fulcrum. The epipharyngeal plate is strengthened by a *median ridge* or *raphé*. Distally the raphé is interrupted and crossed by a *transverse ridge*. On either side of the median a row of fine pores is seen. In every little pore is placed a small seta. The setae turn towards the *oesophagus* and are flexible. Two slender rods stretch from the distal end of the rostrum lateral of the fulcrum. These rods are called the *apodemes* (apod.) and are **S**-shaped with a notched head.



Figs. 5-6.—5. *S. unicornis*, the oral disc fully expanded; 6. *S. unicornis*, the labrum epipharynx and hypopharynx.

The *haustellum* (haust.) or *medioproboscis* (figs. 4 and 5) is the centre part of the proboscis. The *labium* or *theca* forms the principal part of the haustellum. Its wall consists of a loose, flexible membrane, thickened on the anterior and posterior parts into definite plates. The plate on its posterior aspect, the *mentum* or *thyroid* (ment.), covers the whole ventral surface. It is a deeply pigmented, strongly chitinised, cup-shaped plate. Two short, weakly chitinised curved rods articulate to the lower end of the mentum. These rods are called the *mento-furcal bars* (m.f.b.). Their distal end articulates with the lateral processes of the *furca*, an important structure in the base of the oral disc.

The plate on its anterior surface forms the walls of a deep longitudinal groove, the *labial gutter.* The central portion of this plate, forming the floor of the gutter, is thin, especially in its distal two-thirds. Its upper third and its edges are strongly chitinised. This plate is called the *hypoglossa* (hyp. gl.) or *stomal plate.* The strongly chitinised edge of the two plates must be homologous to the two lateral bars which are described by Lowne and Graham-Smith in the blow-fly. Lowne has named these bars the *paraphyses.* The paraphyses terminate in a notched, articular head. In their distal end the paraphyses are pressed together so that the hypoglossa forms a closed tube.



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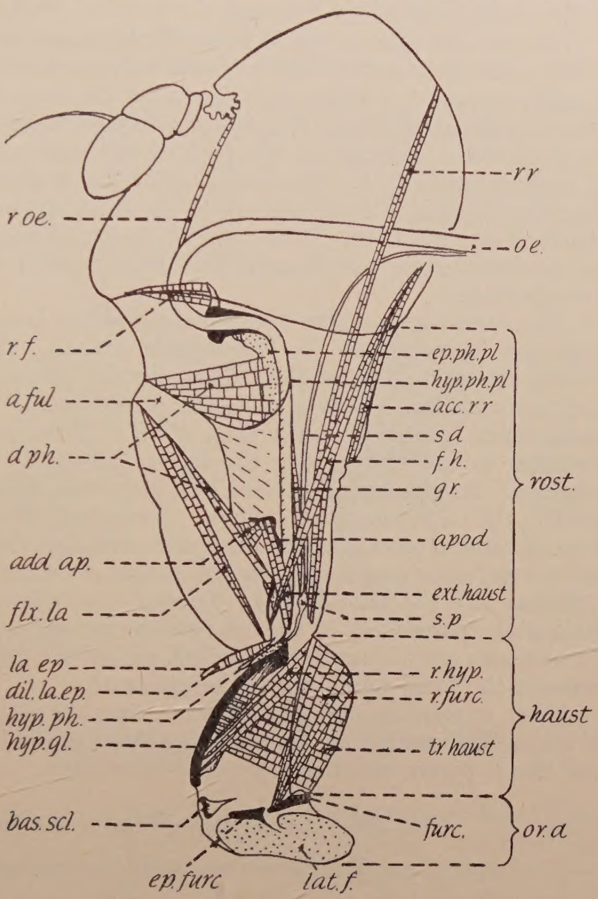

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Figs. 7–8.—7. *S. unicornis,* pseudotracheae; 8. *S. unicornis,* longitudinal section of the head, from the left.

The *labrum-epipharynx* (fig. 6, A, and figs. 4, 5, 8 and 9, la. ep.) is a little tongue that covers a little more than the upper third of the hypoglossa. Its upper end is attached to the border between the rostrum and the haustellum. The border of the tongue is surrounded by a chitinous band which proximally articulates with the apodemes. On its ventral side a deep groove stretches from its base to its tip. This groove continues the dorsal wall of the pharynx; the walls are chitinised. The chitinised wall of the groove fuses in its distal end with the lateral chitinous band. The *hypopharynx* or *ligula* (figs. 6, B, and 8, hyp. ph.) is a little folded, chitinised blade underneath and is surrounded by the labrum-epipharynx, of which it is only one-half in length. It forms an elongation of the ventral wall of the pharynx and is pierced by the salivary duct. Proximally it is produced into two cornua that articulate with the cornua in the ventral end of the fulcrum.

The *oral disc* (figs. 4 and 5) forms the terminal part of the proboscis. It is a soft organ that surrounds the *discal sclerite*—a sclerite formed like a horseshoe the two arms of which articulate with the notched head of the hypoglossa. From the discal sclerite radiate the *pseudotracheae* (fig. 7). The pseudotracheae are six pairs of fine grooves, the walls of which are strengthened by fine arches of unpigmented chitin. The two ends of the arches are free of the disc. By their simple form in *Scatophila unicornis* these organs do not differ from other described EPHYDRIDAE. When the fly desires to suck up a thin layer of fluid, the pseudotracheae are brought into contact with the surface on which the fly is feeding.

The ventral surface (the back) of the oral disc is covered by a pair of weakly chitinised, hairy plates, the *lateral folds* (lat. f.). A strongly chitinised arch is seen above the lateral folds following the border between the haustellum and the oral disc. This arch is the *furca* (furc.). It is composed of three parts firmly connected with each other. These parts are the *body* which stretches transversally along the lower end of the mentum and the *lateral processes*. As already mentioned, two little rods, the *mento-furcal bars* (m.f.b.), connect the mentum with the furca. Two small bars are seen a short distance from the lateral process of the furca and pointing in the same direction. These are the *epifurcae* (ep. furc.). A fine strand stretches from the rear end of the epifurcae into the lateral folds. Laterally, in the oral disc near the notched head of the paraphyses of the hypoglossa, are seen two little triangular plates. These plates are the *basal sclerites* (bas. scl.) of the disc. A fine strand expands between the basal sclerites and the epifurcae.

When at rest, the oral disc is folded along the middle so that the two halves of the surface containing the pseudotracheae are laid against each other. The oral disc is partly withdrawn into the haustellum.

THE MUSCLES OF THE PROBOSCIS (figs. 8 and 9).

(1) *Muscles arising in the head capsule.*

The retractors of the rostrum (Lowne) (= *retractors of haustellum*, Hewitt, 1914 : 59) (r.r.) arise from the occiput. By dissection, it has not been possible to state exactly where they arise. They are long and slender and lie on either side of the middle line behind the fulcrum. They are inserted into the skin of the rostrum near the border of the haustellum. In the blow-fly, they are inserted into the sesamoid sclerites. There are no such sclerites in *Scatophila unicornis*.

The accessory retractors of the rostrum (Lowne) (= *retractors of the rostrum*, Hewitt, acc. r.r.) arise ventro-laterally of the occipital foramen. They are inserted at the middle of the back of the rostrum.

The flexors of the haustellum (Lowne and Hewitt) (f.h.) arise ventro-laterally of the occipital foramen, near the accessory retractors of the rostrum. They are long, slender muscles which are inserted at the lower end of the apodemes. They serve to flex the haustellum to the anterior surface of the rostrum.

The retractors of the fulcrum (Lowne and Hewitt) (r.f.) arise from the anterior edge of the genae and are inserted at the cornua in the upper end of the fulcrum.

Their contraction causes the upper cornua to be drawn forwards and downwards. This again causes the lower end of the proboscis to describe a circular arc backwards.

The retractor of the oesophagus (Graham-Smith) (= *retractors of the fulcrum,* Lowne) consists, so far as I can see, of a single muscle fibre extending from the frontal sack to the oesophagus.

(2) *Muscles arising in the rostrum.*

The dilatators of the pharynx (Lowne) (d. ph.) arise from the internal surface of the anterior arch and lateral plates of the fulcrum and are inserted on the median ridge of the anterior (the dorsal) plate of the pharynx. The muscle fibres from the anterior arch are inserted at the upper part of the median ridge, while the muscle fibres of the lateral plates are inserted on the lower part of the median ridge and at the transverse ridge.

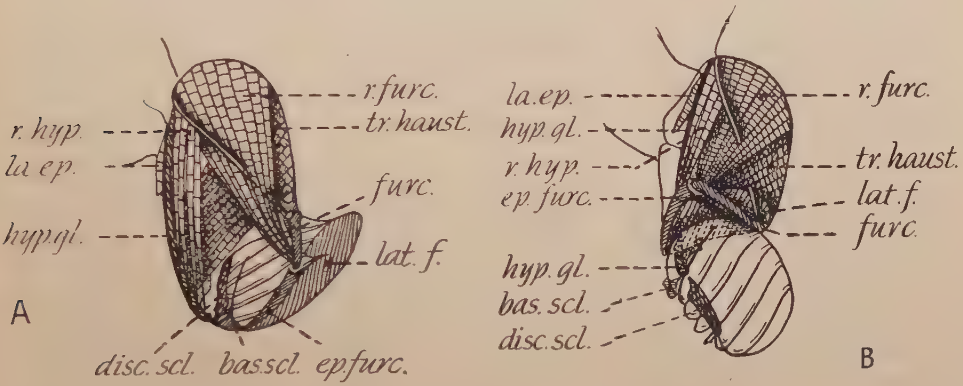

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FIG. 9.—*S. unicornis,* the haustellum and the oral disc: A, in resting position and B, fully expanded.

The adductors of the apodemes (Graham-Smith) (= *retractors of the haustellum,* Lowne; *Accessory flexors of the haustellum,* Hewitt) (add. ap.) arise from the anterior distal margin of the lateral plates of fulcrum and are inserted on the *inner side* of the head of the apodemes. According to Graham-Smith they "seem to assist the extensors of the haustellum by adducting the heads of the apodemes."

The extensors of the haustellum (Lowne and Hewitt) (ext. haust.) arise from the cornua in the lower (distal) end of the fulcrum and are inserted on the *outer side* of the heads of the apodemes. They extend the haustellum on the rostrum by pushing down the apodemes.

These two muscles are very difficult to see because of the structures they overlie. The description is based upon that made by Graham-Smith 1930.

The flexor of the labrum (Lowne and Hewitt) (flx. la.) arise from the lower (distal) end of the anterior arch of the fulcrum and are inserted at the proximal end of the lateral chitinised borders of the labrum-epipharynx near their articulation at the apodemes. By the help of these muscles, the fly is able to lift the labrum-epipharynx from the surface of the haustellum.

The gracilis muscles (Lowne) (gr.) are a pair of very fine muscles that arise from the middle of the ventral plate of the fulcrum and are inserted on the anterior wall of a tiny *salivary pump* (s.p.) on the *salivary syringe* (s.d.). They regulate the flow of saliva.

The epipharyngeal muscles (Graham-Smith) are some fine muscle fibres, described by Graham-Smith, in the blow-fly. According to him, they arise from the hypopharynx and the free portion of the salivary canal and are inserted on the walls of the neighbouring air-sacks of the rostrum. He supposed that they assist in the deposition of the parts during flexion and extension. By the simple dissection used for this study of *Scatophila unicornis* it was not possible to see these muscles.

(3) *Muscles arising in the haustellum.*

The retractors of the hypoglossa (Bolwig) (= *the retractors of the paraphyses*, Graham-Smith) (r. hyp.) arise from the border of the proximal part of the mentum and are inserted by several slips into the distal end of the strongly chitinised border of the hypoglossa. Their contraction causes the hypoglossa to be drawn upwards and inwards into the haustellum. This again causes an extension of the oral disc. They work together with the transverse muscles of the haustellum.

The retractors of the furca (Lowne and Hewitt) (r. furc.) arise from the proximal halves of the inner surface of the mentum and are inserted at the lateral processes of the furca.

Contraction of these muscles causes the surface of the oral disc carrying the pseudotrachea to be folded out. The action is brought about by the arms drawing the epifurcae, and with them the lateral folds, upwards and backwards. This causes the edges of the oral disc to describe an arc of a circle outwards and thus they expand the inner (dorsal) surface of the oral disc.

The transverse muscles of the haustellum (Lowne) (= *dilatator of the labium-hypopharynx*, Hewitt) (tr. haust.) arise from the middle line of the mentum between the centre and the distal end and are inserted at the strongly chitinised borders of the hypoglossa. Their contraction causes the hypoglossa to be drawn towards the mentum. This causes the extension of the oral disc.

The dilatators of the labrum-epipharynx (= *praelabral*, Lowne) (dil. la. ep.) are very short muscles arising from the chitinised borders of the labrum-epipharynx and are inserted in the chitinised walls of the median groove on its ventral surface. They are believed to regulate the diameter of the groove.

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THE EFFECT OF PYRETHRUM ON THE SPIRACULAR MECHANISM OF INSECTS

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It has long been recognised that pyrethrum acts primarily on the nervous system of insects. Krüger (1931) showed that the ganglia and nerves of *Corethra* larvae exposed to pyrethrum become vacuolated. Wilcoxon and Hartzell (1933) describe various degenerative changes in the ganglia of mealworms treated with pyrethrum; and Hartzell (1934) confirmed these observations on *Melanoplus*. Recently F. H. Drummond (unpublished), working at the Imperial College of Science, has made a thorough histological study of these changes.

In the course of the present work sections of the thoracic and abdominal ganglia of normal adults of *Rhodnius prolixus* were made and their appearance compared with that in adults which, though still alive (as indicated by the action of the heart and the gut and by occasional movements of the legs), had been paralysed by treatment with pyrethrum 10 days previously. Fig. 1 shows approximately corresponding areas in the ganglia. In the pyrethrum-treated insect (fig. 1, B) the ganglionic mass is greatly shrunken, few cells are recognisable, and the greater part consists only of amorphous, granular material containing a few scattered vacuoles.

This destructive action on the central nervous system is reflected in the paralysis of the insect. Within a few minutes of the application of the pyrethrum to the cuticle, the movements become unco-ordinated, and within a few hours almost all movement ceases.

The cause of death in insects poisoned by pyrethrum is unknown. Since, however, it is a nerve poison, it seemed likely that it might lead to paralysis of the spiracular sphincters, the muscles of which are controlled by the central nervous system. In the living insect these sphincters are held closed most of the time; after death they are relaxed and open. Their chief function is to prevent loss of water by evaporation from the tracheal system: if they are caused to open by exposure to air containing 2 per cent. or more of carbon dioxide the insect loses water at a rapid rate (Mellanby (1934), Wigglesworth and Gillett (1936)) and, in a dry atmosphere, it quickly dies.

It therefore occurred to me that the cause of death from pyrethrum might be desiccation as the result of interference with the spiracular control. Two methods were employed to test this possibility. The loss of weight in insects poisoned with pyrethrum was compared with that in normal insects, and the movements of the spiracular sphincters were observed directly.

Loss of weight after treatment with pyrethrum.

A number of adults of the large blood-sucking bug *Rhodnius prolixus* were fed, and twenty-four hours later the anus of each was occluded with paraffin wax in order to prevent loss of water by excretion. Half were treated with pyrethrum and half kept as controls, both lots being exposed to 0 per cent.

relative humidity at 25° C. and weighed daily. An extract of pyrethrum in a highly purified liquid paraffin, containing 2 per cent. pyrethrins, was applied as a thin film to the antennae. Within half an hour the movements in the treated insects become unco-ordinated. After one hour unco-ordination is complete; the bugs are unable to walk properly, and spasmodic contractions of the muscles occur. At the end of twenty-four hours the insects are almost incapable of any movement, and sometimes they can be recognised as living only by the pulsations of the heart. In this state many will survive for ten or twenty days, others die after two or three days.

Table I.

Loss of weight in milligrams on successive days after commencement of experiment.

Days	1	2	3	4	5	6	7
Pyrethrum treated	3·3	3·5	*8·2*	*9·4*	*9·4*	*9·4*	*8·0*
	4·9	3·2	3·4	2·2	2·2	2·2	1·8
	5·1	3·5	*8·5*	*8·5*	*8·5*	*8·5*	
	5·2	1.5	*7·5*	*7·5*	*7·5*		
Normal controls	1·8	2·2	1·7	1·7	1·7	1·8	
	0·8	3·0	2·0	0·9	0·9	0·9	2·2
	1·9	2·1	1·0	3·3	3·3	3·2	

Table I shows typical examples of the changes in weight in these insects. The figures in italics represent weighings made after death as indicated by the cessation of the heart beat. During the first day the loss of weight in the pyrethrum-treated insects is sometimes rather greater than in the normal. Perhaps this is due to the spasmodic muscular contractions during the early stages of poisoning; for it is well known that muscular activity leads to more frequent opening of the spiracles (Hazelhoff (1927), Wigglesworth (1935)). But thereafter the loss of weight does not differ from the normal until death has occurred. It then shows a two- or three-fold increase to 7·5 or 9·4 mg. per diem. Under conditions approximately the same Wigglesworth and Gillett (1936) showed that *Rhodnius* adults in which the spiracles are kept permanently open by exposure to dry air containing 10 per cent. of carbon dioxide lose from 9 to 12 mg. per diem, the total weight of the insect varying with the amount of blood in the stomach from 100 to 200 mg.

From these results it is evident that the loss of water by evaporation does not become excessive in insects treated with pyrethrum until *after* death.

Movements of spiracles in insects treated with pyrethrum.

The opening and closing of the spiracles in the living insect is most readily observed in the flea examined by transmitted light (Wigglesworth, 1935). But it is difficult to apply pyrethrum to the flea without contaminating the whole body including the tracheal system. For the present purpose the adult bed-bug *Cimex lectularius* has therefore been used.

Fig. 2, A, shows the closing mechanism in the spiracle of *Cimex*, which is on the same principle as that described by Mammen (1912) in *Pyrrhocoris*, and fig. 2 B, B′ shows the spiracle in the open and closed positions as seen by transmitted light in the living insect. The opening and closing is not always so easy to observe as in the flea, but in some specimens at least the exact degree of opening can be clearly seen.

In the normal adult *Cimex* the spiracles remain closed for the most part, and make only slight quivering movements which open a minute cleft in the spiracle from time to time. They open widely in about a minute and remain open, if the insect is submerged in water. When the bug is examined in the gas chamber previously described (Wigglesworth, 1930, 1935) in air containing 10 per cent. carbon dioxide, they open fully.

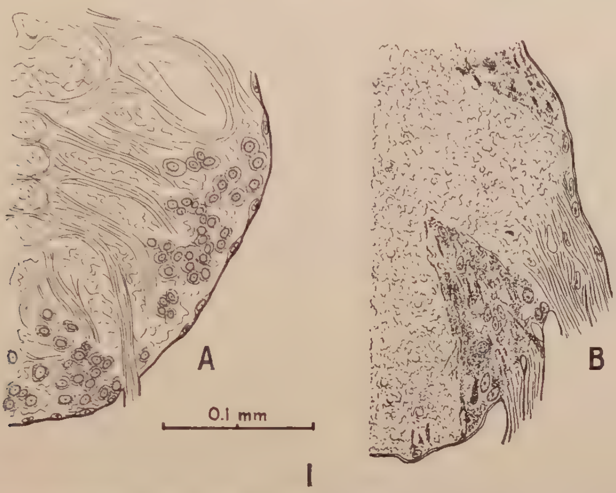

Fig. 1.—Horizontal sections through the fused abdominal ganglia of *Rhodnius prolixus* adult. (Fixed Carnoy, cut in celloidin and paraffin, stained haematoxylin.) A, normal adult. B, living adult paralysed 10 days with pyrethrum in liquid paraffin applied to antennae.

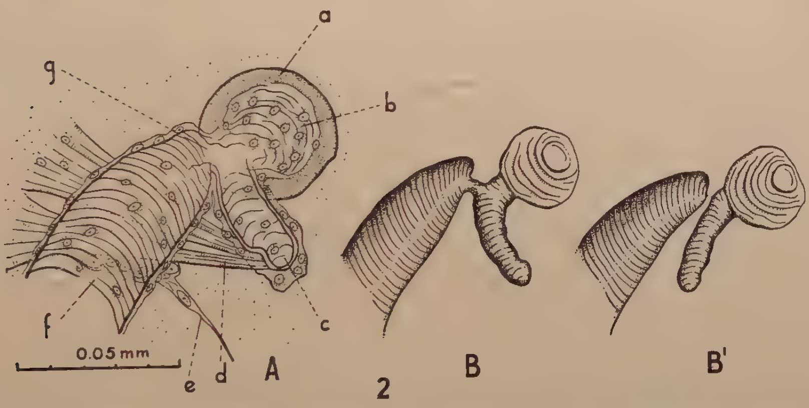

Fig. 2.—A, closing mechanism in abdominal spiracle of *Cimex lectularius* viewed from inside. *a*, peritreme; *b*, atrium; *c*, thick-walled diverticulum serving as a lever to close the tracheal orifice; *d*, muscle running from tip of lever to cuticle of abdominal wall; *e*, nerve, ending in group of cells applied to the muscle; *f*, trachea; *g*, tracheal orifice. B, spiracle as seen by transmitted light in the living insect, open position; B′, the same, closed position.

A thin film of the same pyrethrum extract as before was applied to the antennae of *Cimex* adults. They were quickly paralysed; after twenty-four hours *very* slight movements of the limbs might be seen on watching closely; but the movements of the heart and gut continued normally and the insect might remain alive for a week in this state. Others treated in the same way died in two or three days.

During the early stages of paralysis, when spasmodic twitchings of the muscles are taking place, it sometimes seems as though the spiracles are opened rather more widely than in the normal insect. But later, when paralysis is complete, they show little movement, remaining closed most of the time. On flooding with water or on exposure to 10 per cent. carbon dioxide the spiracles slowly open and remain open until restored to air. After death the spiracles open.

Discussion.

It is thus clear that at a time when the insect is almost completely paralysed and when histological examination of the nervous system shows that extreme degeneration has taken place in the ganglia, the spiracles are still functional. They are held closed and prevent evaporation of water; and they open in response to the usual stimuli. It is possible that the sensitivity of the response is reduced, but this has not been established.

It is worth recalling in this connection that Hazelhoff (1927) showed that the isolated spiracle of the cockroach will still respond to carbon dioxide, and in the flea (Wigglesworth, 1935) slow responses in the spiracle can be obtained after the central nervous system has been completely removed.

The cause of death after pyrethrum poisoning therefore remains obscure. Where an insect requires food at frequent intervals it may well die of starvation in its paralysed state. But there must be some general poisonous action in addition, for *Rhodnius* treated with pyrethrum will die in from 2 to 20 days; whereas the normal insect will resist starvation for 10 weeks or more.

Summary.

The destructive action of pyrethrum on the central nervous system of insects is confirmed. But it is shown that in *Rhodnius* there is little or no increase in evaporation from insects paralysed with pyrethrum until after death; and that in paralysed *Cimex* the spiracles are kept closed and still react to carbon dioxide. Desiccation cannot therefore be the main cause of death after pyrethrum poisoning.

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THE SHAPE AND DISTRIBUTION OF THE FACETS IN AN ARTHROPOD'S EYE AND SYSTEMS OF POINTS ON THE SPHERE

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Communicated by Dr. V. B. Wigglesworth, F.R.S.

The irregularity in the shape and distribution of the facets of an arthropod's eye are considered in the literature from the point of view of division of labour, or as inherited anomalies. In the first case the interrelation between the size of the facets and the optical acuity in the different regions of the field of vision are investigated (Plate, 1926), in the second case deviations from an intuitively conceived regular form. Such investigations are made under the assumption that regular distribution and shape of facets are possible. Some authors, especially in older morphological treatises, dwell on the great regularity of the hexagons. Closer investigation cannot accept " regularity " without defining it. We have tried to crystallise the intuitive conception of regularity, and plausible definitions can be made; but it appears then that completely regular figures of facets cannot exist at all. A limited regularity leads to configurations which might be suitable to describe the actual distribution. It appears that places of disturbance must necessarily occur, which corresponds to the observation. The geometrical formulation of the problem is of mathematical interest apart from its morphological application.

Two remarks concerning the physiology and development of a facet eye might be useful:

The physiologist expects for reasons of economy that a mosaic apparatus produces an image which is composed of little images as similar in size as possible and as closely packed as possible. Apart from the privileged parts of fields of vision referred to above such a mosaic of images is produced by an aggregation of many equal and maximally packed single eyes, the surfaces of which are the corneal facets of the complex eye. For the purpose of this paper the spatial configuration of the coniform single eyes towards the centre of the total eye can be neglected.

During the development of the facet eye in a holometabolic insect, for example a fly, the subdivision and differentiation of the ommatidia take place in one single developmental phase more or less simultaneously. In a hemimetabolic insect, for example a stick insect, younger larvae show fewer facets in the eyes than older larvae and imagines. The accrescence starts from several centres of growth which are situated on the margin of the eye during the single steps of metamorphosis. In both cases a larger number of facets grows " simultaneously." It is possible to regard the final shape and distribution of the facets as a result of the competition between the single growing ommatidia.

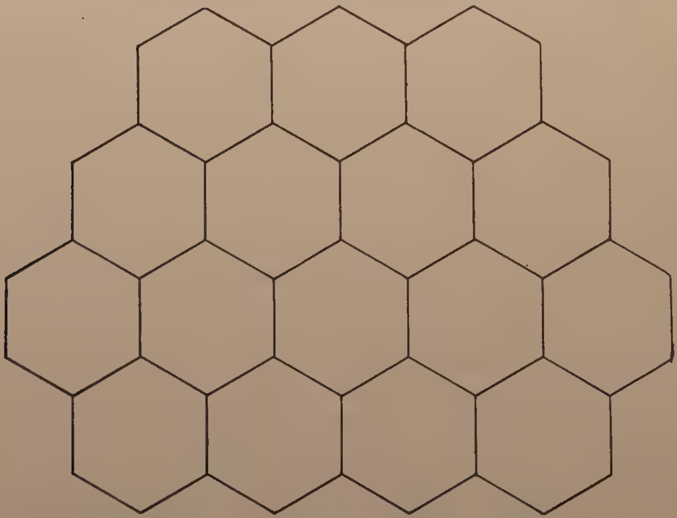
The simplest mathematical approximation of an insect's eye is presumably a subdivision of the surface of the sphere, or of a reasonably large section of it, into a network. The lines of the network represent the border lines of the corneal facets and meet in the meshes of the net. We call such a curved figure as we draw it on the sphere, a polyhedron. In general its surfaces, the facets, are hexagonal. One might think that the problem is to draw a hexagonal polyhedron on this sphere. Now it is probably since the time of Plato but certainly since that of Euler, well known (Steinitz and Rademacher 1934) that hexagonal polyhedrons on the sphere do not exist. But this theorem does not touch our problem. In fig. 1 may be seen a part of a plane covered with hexagons, and it is naturally possible to regard this as a projection of a piece of a sphere's surface. Euler's theorem concerning the non-existence of hexagonal polyhedra anticipates that in each corner three or more edges meet. The marginal polygons in fig. 1 must therefore be regarded as pentagons, one side of which has got a bend. The whole is a " topological " problem and the more or less regular form of the lines and faces is unimportant.

Our problem, however, is a metrical one; it is easy to demonstrate, and well known, that the surface of a sphere cannot be covered with regular hexagons. The angle of a regular spherical hexagon is bigger than 120° and the surplus is $\frac{1}{6}$th of the area of its face. Regular hexagons of equal or different sizes can therefore be arranged on the sphere only in such a way that only two have a corner in common. One could, of course, distribute equal regular hexagons on the sphere which would not touch each other, but that cannot possibly be a model of an insect's eye. An absolutely regular distribution would demand that the centres of the hexagons are regularly distributed, leaving aside the problem of how the hexagons are placed around these centres, and what is to be regarded as a centre, for example the centre of gravity.

By implication also the limits of the single eye which results from the competitive growth already mentioned must at first be omitted.

The first question is therefore: Is it possible to distribute n points absolutely regularly on the sphere? This question occurs also if one tries to produce an intuitive model of the lines of force radiating from a pole.

A first proposition: to regard the corners of a regular polyhedron as regularly distributed on the circumscribed sphere gives a solution only for



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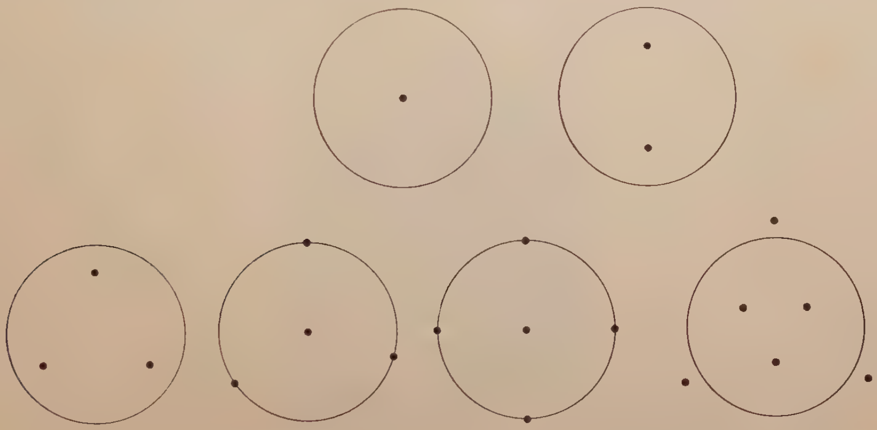
$n = 4, 6, 8, 12, 20$, in addition to the dihedrons (doubly covered regular polygons) which anyway are unsuitable for a large value of n: in a dihedron all points accumulate on the equator and there is nothing around the poles. Although there exist eyes consisting of only a few facets (the ant *Solenopsis*, 6–9 facets; the silver fish *Lepisma*, about a dozen facets) the number of facets is generally large, sometimes very large (the dragonfly *Aeschna*, 10,000 facets, the beetle *Necrophorus*, 30,000). Therefore the theory cannot remain confined to five single values of n, and another approach to the problem must be tried.

By geometrical abstraction we perceive that the centres of the spherical discs grow simultaneously and with equal speed and that they stop growing when the maximum radius is reached. Therefore we do not postulate *a priori* a "regular" distribution as was done by Finsterwalder[1] (1936). This definition can be put in several other ways:

Spherical discs of equal size are placed on the sphere in such a way that they do not overlap and the uncovered surface becomes a minimum.

Or: n points on the sphere determine $\frac{1}{2}n\ (n - 1)$ distances measured as shortest distances between the centres.



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How are the n points to be arranged so that the shortest of the distances is a maximum? (Blumenthal, 1939).

These definitions are rigorous forms of what we called, starting from biological considerations, "as similar size as possible" and "as closely packed as possible." The last definition is the most practicable. It is also possible to take instead of the complete sphere a reasonably limited section of it, for example, a region ("Gebiet") in the geometrical sense corresponding to the real complex eye. In this form our problem is a generalisation of a problem described by Fejes (1940), who deals with an analogous problem for a large n in a plane region. A similar problem can also be found in a publication by Kershner (1939); the covering of a region with circles of equal and maximally small circles which of course do overlap.

The problem of locating n points the minimum distance of which reaches a maximum has always a solution; sometimes, for example when $n = 5$, several solutions. It is presumably very difficult to find a general solution for

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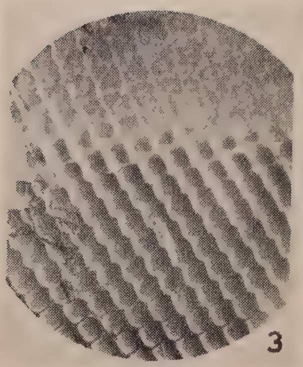
[1] Finsterwalder chiefly considers distributions in which no point of the system is outstanding.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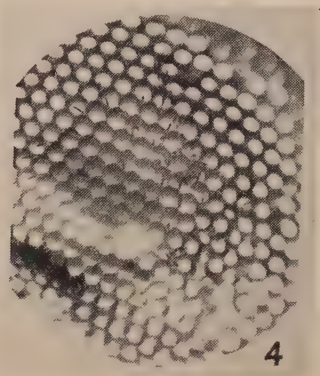
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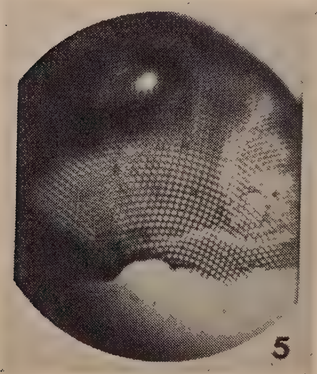
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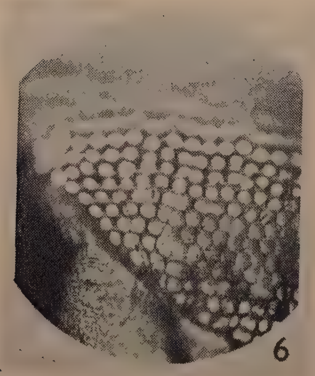
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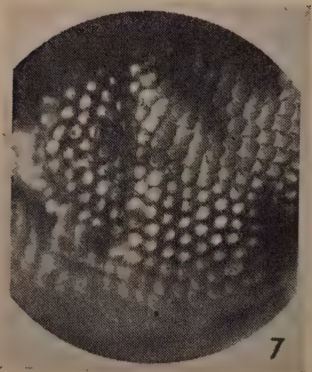
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all values of n, and maybe it is as impossible as the exact description of the growth of a number-theoretical function. A description of the solutions for $n = 2, 3, 4, 5, 6$, and 7 follows and $n = 8, 12$, and 20 will be touched on (fig. 2).[2]

Fig. 2 gives the solutions in stereographical projections (central projection from the north pole towards the equatorial plane). The circle is always the equator, one point of the system is in the north pole and its projection therefore disappears to infinity. One of the points nearest to the pole is placed in the 0 meridian. For $n = 3$ the solution is an equilateral triangle; for $n = 4$ the points are at the corners of a regular tetrahedron (in accordance with Blumenthal), for $n = 5$ the solution consists of the north and south poles and three points on the equator which are at least a quadrant distant from one another. The solution for $n = 6$ is the corners of an octahedron; for $n = 7$ for the first time greater difficulties are experienced, the minimum distance is the side of an equilateral spherical triangle the angle of which is 80°. The most likely solution for $n = 12$ is the corners of a regular ikosahedron.

The solution for $n = 8$ is not the corners of a cube which do not give the maximum of the minimum distance. The corners of an Archimedean Antiprism with square bases are nearer the solution or perhaps the solution itself. Analogous to this, the solution for $n = 20$ is not the corners of a dodecahedron. Details from a geometrical point of view will be published later.

TABLE 1.

n	Maximum of the minimum angular distance
2	180°
3	120°
4	109° 28′ 16″
5	90°
6	90°
7	77° 52′ 10″
8	74° 51′ 31″
12	63° 26′ 06″
20	45° 26′ 19″

It is certain that the configuration of maximal density for big values of n cannot be arranged in a net of equilateral triangles in the neighbourhood of every point. This configuration is only possible if one joins the centres of regular hexagons covering a plane. On the sphere the existence of exceptional places where the "Wabenzellen" have fewer than six sides is necessary. That can be proved as follows: The "Wabenzelle" round one point a of the system means the aggregate of all points which are nearer to a, or at least not farther from it, than from all other points of the system. We call a and b adjacent points if the corresponding cells have one side in common. The shape of the cells satisfies the presuppositions of Euler's theorem, mentioned on p. 16: all boundaries are arcs of great circles. If we exclude systems, where all points are arranged on one great circle, which can be done for $n = 4$, no cell is constituted by two arcs of great circles. Then the following formula is valid (*see* Steinitz):—

$$\text{(i)} \qquad 3f_3 + 2f_4 + f_5 \geq 12 + f_7 + 2f_8 + \cdots$$

where $f_k =$ the number of cells with k corners. As in (i) the right side ≥ 12

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[2] A limited number of arrangements in space is found in the covalencies of a polyvalent atom, resulting in a few stereochemical types (Sidgwick and Powell, 1940).

there must be at least 4 points on a sphere, which are adjacent to fewer than 6 points. Consequently, we expect on a whole sphere at least 4 centres of disturbance, where the points deviate from the triangular pattern and are arranged almost rectangularly. In these regions, where the network is only slightly different from a square one the Wabenzellen are hexagons with one pair of very short sides; consequently they possess rectangular appearances. On the surface of an arthropod eye covering the major part of a sphere, one or more of such regions must occur. This may be confirmed by observation. Fig. 3 shows a region of a complex eye of *Drosophila* where this configuration appears. In fig. 4 a piece of the surface of the same eye is reproduced showing the familiar hexagonal pattern. Fig. 5 shows both arrangements in a housefly.

It appears from these considerations that the configurations of facets in abnormal eyes due to mutation constitute a different problem. In the normal eye the forces involved are so well balanced that rougher local deviations from " regularity " do not appear, but disturbances in this balance occur in mutant races of several *Drosophila* species. In these the shape and arrangement of the facets is far from regular, polygons possessing more than six sides are frequent, and make possible the existence of polygons with fewer sides (figs. 6 and 7).

In conclusion we should like to express our thanks to Professor J. B. S. Haldane for his help and interest.

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BOOK NOTICE.

A Text-Book of Zoology. By T. J. PARKER and W. A. HASWELL. 6th edition in 2 volumes. Volume 2, revised by C. FORSTER-COOPER. 8vo. London (Macmillan) 1940. pp. xxiii + 758; 656 figs. Price 36*s*.

This is the second volume of a work noticed in the last volume of these *Proceedings*, and is devoted to the Chordata.

The general plan of this well-known work remains unaltered and new material has been added wherever it seemed best to fit.

A new classification of Fishes is introduced, and the former chapters on geographical distribution, the philosophy of Zoology, and on the history of Zoology are absent from this edition.

There is a remarkable list of periodicals of which the use is not clear and some entries are bad examples of " made-up " titles.

The index occupies 58 pages of treble-column matter.

AN INTERESTING CASE OF DEVELOPMENT IN CERTAIN SOUTH AMERICAN HESPERIIDAE (LEP. RHOPALOCERA)

By Brigadier W. H. Evans, C.S.I., C.I.E., D.S.O., F.R.E.S.

Some of the handsomest Hesperiids in the world appertain to the American subfamily Pyrrhopyginae and my interest therein was aroused by the investigations of Mr. E. L. Bell of New York, which appeared in 1931 (*J. N.Y. ent. Soc.* 39). He found that in the *phidias* group of the genus *Pyrrhopyge* specimens apparently belonging to the well-known species *phidias* and *bixae* could be separated by the very different genitalia into 2 or 3 species and that in certain cases the genitalia of a *phidias*-like species exactly resembled those of a *bixae*-like species.

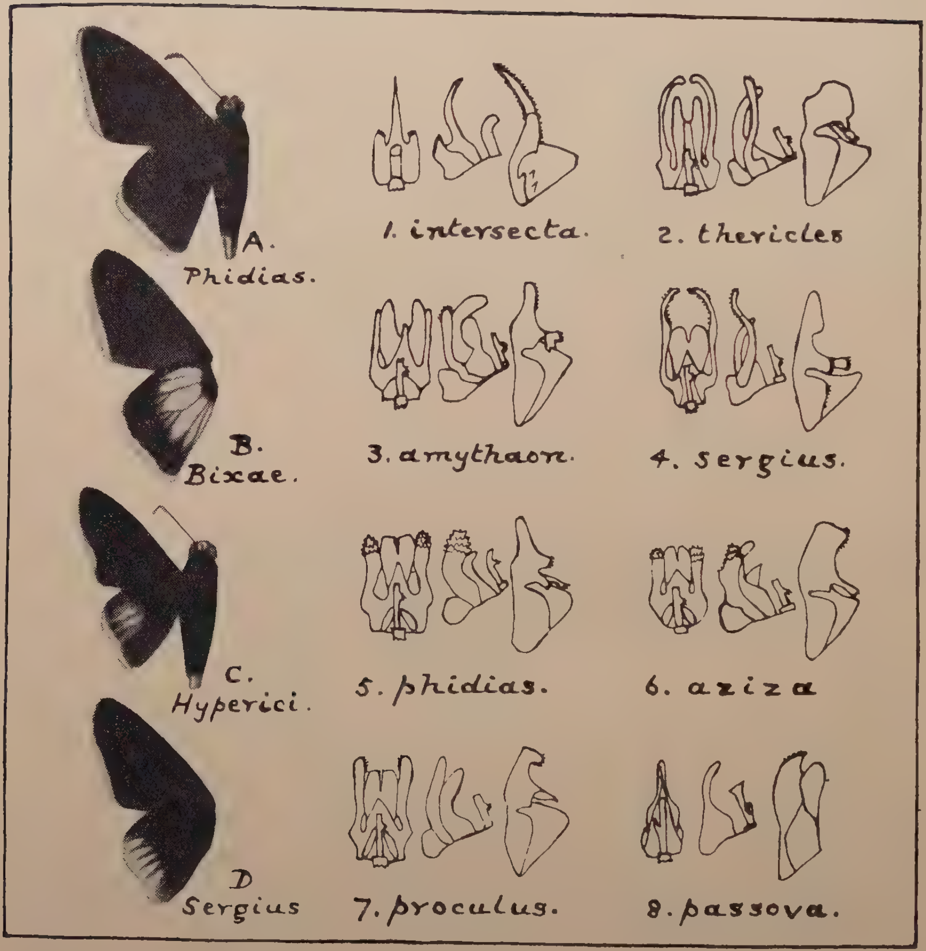
The group consists of large dark blue insects with a wing expanse of 2 to 2½ inches: they all have red heads and red tails to the abdomen and the cilia of the wings are usually pure white. There are four well-marked types of facies, viz.:

A. *phidias*: plain dark blue above and below.
B. *bixae*: resembling *phidias* above, but with a well-marked basal white band on the hind-wing underside.
C. *hyperici*: resembling *bixae* below, but with a large pale blue area on the upperside of the hind-wing.
D. *sergius*: resembling *phidias* above, but with a broad submarginal white band on the hind-wing underside.

I collected together some 650 specimens of the group in the British Museum in London and from the Zoological Museum, Tring. My investigations in respect of specimens of *phidias*, *bixae* and *sergius* types confirmed and extended Mr. Bell's results. He had found only one species of the *hyperici* type and I did not anticipate finding any more. My first dissection agreed with Bell's. As a check I dissected a second specimen which appeared to diverge in facies from the first more than did the rest of the series of 40 I had before me. Its genitalia were quite different so I dissected up the whole series and eventually found that there were 8 quite distinct species.

This, however, is by no means the whole story. I had obtained similar results in Oriental genera. For instance, in the genus *Potanthus* I had found many more than eight species looking alike, but with quite different genitalia. I found that every one of the genitalia was repeated in the *phidias* and *bixae* types, while three of them occurred in the *sergius* type. I then arranged examples of each form in horizontal rows according to the wing pattern and in vertical rows according to the genitalia pattern and came to the conclusion that there were 8 perfectly distinct species, each with 3 or 4 wing patterns.

I then found that the *hyperici* form of each species occurred only in Para and the lower Amazon region and that the other forms were absent in that area. Specimens from Guiana and eastern Venezuela were always conspicuously smaller, while the termens of both wings were excavate and the flanges on either side of the uncus were shorter. In British Guiana and eastern Venezuela the *phidias* type only occurred, while all specimens from French Guiana belonged to the *bixae* type. The *phidias* form occurs generally from Colombia to Bolivia, while one species (*phidias*) extends to Mexico, having slightly modified genitalia in Central America. The *bixae* form seems to occur


A.
Phidias.
B.
Bixae.
C.
Hyperici.
D
Sergius
1. intersecta.
2. thericles
3. amythaon.
4. sergius.
5. phidias.
6. aziza
7. proculus.
8. passova.

with the *phidias* form from Colombia to Peru, but generally the white band is very much wider in Colombia than it is in Ecuador, Peru and Bolivia. The *sergius* form seems to be confined to Peru, just reaching into Ecuador and Bolivia, but *phidias* forms from British Guiana show an approach to the *sergius* type, particularly in the species *phidias*: this tendency is entirely absent in specimens from Trinidad.

In the genitalia diagrams the left-hand figure in each case represents the central view of the uncus and the aedeagus. The central figure shows the uncus and the aedeagus viewed from the left. The right-hand figure shows the inside of the left clasp. It will be observed that the genitalia of No. 1 species, *intersecta*, are totally different in all respects from the genitalia of the other 7 species, and particularly so in respect of the aedeagus as shown on the right of the central figure. The wings in this species are rather more prolonged and there is a slight difference in the hind-wing venation about the lower end of the cell. I consider that the species should be separated generically from the remainder. There are several other species now included in the genus *Pyrrhopyge* which have very similar genitalia and would accompany *intersecta* into the new genus. Also, strange to relate, there are some species in what are considered to be widely separated genera, viz. *Jemadia*, *Mimoniades*, and *Sarbia*, which have similar genitalia and consequently should be considered congeneric with *intersecta*.

It will also be noticed that the genitalia of No. 8, *passova*, are entirely different from the rest: here again particularly in respect of the aedeagus, which is bifid. In this case there are other structural differences: the antennal club is differently shaped, the hind-wing is tornally lobed and secondary sexual characters are present in the legs. I have no hesitation in separating this species generically from *Pyrrhopyge*. All the forms can be at once separated from the remaining species by the presence of a conspicuous red area at the tornus of the hind-wing.

The *bixae* and *hyperici* forms of the first species *intersecta* can be readily distinguished by the extension of the hind-wing white band on the underside to the fore-wing. The same forms in No. 7, *proculus*, have a white basal streak along the costa of the fore-wing on the underside.

The *hyperici* forms for each species can be readily separated by the shape of the blue area on the upperside of the hind-wing as well as of the white area on the underside.

The *sergius* form of No. 6, *aziza*, has the submarginal white band on the hind-wing underside appearing also on the upperside.

For the remaining forms of each species dissection of the genitalia is the only certain means available for identification, though the amount of red colouring in the head and the blue shade of the ground-colour of the wings is often of assistance.

I can offer no explanation of the remarkable development which I have described. Perhaps there is something in the climate of Para that induces the blue coloration on the upperside of the hind-wing. Or the cause may be some chemical factor in the food-plant dependent perhaps on the geological formation. Since no Hesperiid, as far as is known, is "protected," I am afraid the mimicry theory cannot be applied. In this connection it may be remarked that many species of the PYRRHOPYGINAE are, shall one say, "mimicked" by species in other subfamilies of the HESPERIIDAE, the most noteworthy being a species of the genus *Pyrrhopygopsis*, which displays both *phidias* and *bixae* forms. This, however, is a very different subject, which cannot be discussed further at present.

MATING AND OVIPOSITION IN *CNEPHASIA CHRYSANTHEANA* (DUP.) (LEPIDOPT., TORTRICIDAE)

By J. A. Reid, F.R.E.S.

Some trials made by Dr. O. W. Richards had indicated that it was difficult to get species of *Cnephasia* to mate in captivity, at least in rather small containers. Therefore in the first attempts to secure mating of *C. chrysantheana* the moths were confined in as large a space as possible. A window embrasure 8 feet long, 5 feet high and 1 foot deep was chosen, the open side facing the room being closed with muslin. In this space freshly emerged females were found to mate fairly readily when left overnight with about an equal number of males; of 17 ♀♀ about 3 later proved infertile. The fertilisation of a female was shown by dissection and examination of the bursa, when the presence or absence of a spermatophore could be seen.

Since *C. chrysantheana* mated quite freely in the window embrasure, it was decided to try smaller containers, as the former was inconvenient to use. Subsequently when females were required for oviposition experiments they were put in a wooden box 2′ × 1′ × 1′ with a glass front, two sides of muslin, and a sliding door at one end. Altogether a total of 60 females were put in this box to mate, and of 54 recovered, 42 proved to have mated and 12 had not. Smaller containers were also tried in order to see if the size of the container affected the ease with which mating occurred and it was found that it did, as can be seen from Table I. Owing to the comparative scarcity of the males it was not always possible to get equal numbers of the sexes, and some of the males had mated once before, but as it is shown later that males can mate on two successive nights, the figures show that mating does not occur at all readily in small containers.

Attempts were made to get *C. virgaureana* (Treits.) and *C. pascuana* (Hb.) to mate but without success. *C. pascuana* was tried in the window embrasure; *C. virgaureana* was tried in the box, in large glass jars, etc., both indoors in the laboratory, in a constant temperature room and out of doors. Some of the females that were kept laid a few eggs, but these were infertile and dissection subsequently showed that the moths had not mated.

As soon as it was discovered that *C. chrysantheana* would mate in captivity it was decided to try and find out the egg number. For this purpose the following method was evolved. Females that had emerged during the previous 24 hours were put in the glass-fronted box mentioned earlier with about an equal number of males. The following morning the females were removed and placed singly in 3 × 1-inch tubes closed with corks that had two furrows cut in the sides to provide ventilation. A piece of cotton wool, on which a few drops of a strong cane-sugar solution had been placed, was pinned to the underside of each cork and a strip of blotting-paper put in each tube for the moths to oviposit on. The moths, though having rather short tongues, were seen to take the sugar-water freely, and the impression was gained that whenever they came in contact with it or very close to it, the tongues were extruded automatically as a reflex action. The great majority of the eggs were laid on the blotting-paper, and the strips were removed each day, the eggs on them counted, and fresh pieces put in the tubes. By counting the eggs on the blotting-paper and the few that were laid on the corks and the glass, it was possible to keep a record of the number of eggs laid by individual moths each night.

The strips of blotting-paper from the different days were kept apart so that the incubation period of the eggs could be determined. In a series that were given no sugar-water, the majority of the eggs were laid on the underside of the corks and not on the blotting-paper; evidently the moths given sugar-water were prevented from behaving similarly because of the damp cotton wool.

It was not possible to tell whether any eggs were laid in the box on the night of mating, so separate experiments were made to settle this point. A fresh pair of moths was put in each of two large glass jars (the dimensions of one are given in Table I) and the mouths of the jars closed with muslin. The following morning the jars were examined and no eggs were found in either; one female was later shown to have been fertilised. The experiment was next repeated on a larger scale, 5 fresh females being placed in each jar and again no eggs were found the following morning, although 7 of the 10 females were later shown to have been fertilised. It was therefore concluded that no appreciable number of eggs is laid on the night of mating and that consequently the females laid all their eggs in the tubes. Presumably an appreciable time elapses between the placing of the spermatophore in the bursa and the completion of migration by the sperms from the bursa into the spermatheca. Possibly the time taken by this migration may account for the fact that no eggs are laid on the night of mating, although the examination of some spermatophores the morning after mating failed to reveal any sperms, which were, however, plentiful in the spermatheca.

Table I.

Container	No. of moths		No. fertilised after 2 nights
	♀♀	♂♂	
Glass jar, 1′ high, 8″ diam.	6	5	4
Zinc and glass breeding cage, 11″ high, 7″ diam.	6	6	2
Glass jam jar, 1 pound size	6	3	2
7 glass tubes, 3″ × 1″, corked, 1 pair of moths per tube	7	7	1

The day-by-day oviposition record for 19 fertile females given sugar-water is shown in Table II, which also shows the total number of eggs laid by each moth and the length of life in days. The temperature was uncontrolled and varied between 17° and 21° C. After death each moth was dissected and the condition of the ovaries noted; the last column of the table gives the approximate number of mature eggs found in the ovaries. At the foot of the two previous columns the mean number of eggs laid by one moth (300) and the mean length of life 14·6 days are shown. The figures in this table should be compared with those of Table III, which records the same data for five fertile females that were not given any sugar-water; the differences are striking. The mean length of life of the starved moths was only about one-third that of the others and the mean number of eggs laid a little more than a half; the egg number was therefore less affected by starvation than the length of life. The values for the daily egg numbers of the starved females during the first three days are much the same as for those given sugar-water; there is one record of 110 eggs on the third day and there are only three records of over 100 eggs in a day from one moth of those given sugar-water. The last column of Table III shows that at death the ovaries of the starved moths were empty, or almost

TABLE II.

Oviposition, etc., in moths given sugar-water.

No. of ♀	Days from commencement of experiment																		Total eggs laid	Length of life in days	Approximate no. of mature eggs left in ovaries
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18			
	No. of eggs per day																				
1	3	51	110	39	46	31	24	19	11	7	0	0	D0						341	13	30
2	0	0	0	2	10	87	0	1	63	1	0	0	11	1	1	D0			177	16	60
3	32	40	43	27	23	33	14	15	15	12	18	7	5	D0					284	14	6
4	68	7	35	55	69	49	24	24	10	7	30	12	10	D0					400	14	7
5	0	17	89	85	65	56	31	36	23	17	0	9	28	8	9	5	4	D0	482	18	2
6	28	33	0	0	2	21	33	9	32	3	24	20	20	37	25	11	0	D0	298	18	40
7	49	55	44	20	16	25	21	0	0	3	0	0	0	0	0	0	D0		233	17	40
8	65	51	64	47	46	30	27	27	17	17	13	15	15	10	11	D0			455	16	4
9	41	89	54	32	49	36	37	22	17	13	10	0	0	D0					400	14	3
10	1	2	4	17	114	52	28	30	14	26	11	3	D0						302	13	10
11	0	0	1	8	52	70	27	50	29	33	20	4	D0						294	13	20
12	0	0	0	2	47	90	0	0	0	0	D0								139	11	22
13	1	8	10	70	85	35	11	35	33	0	24	22	0	D11					345	14	6
14	1	48	49	38	28	23	23	21	5	15	12	6	8	7	D0				284	15	3
15	49	22	19	22	19	23	18	12	12	10	10	11	10	7	6	4	7	D0	261	18	12
16	2	4	8	0	10	102	40	18	9	4	D0								197	11	33
17	74	36	11	11	10	2	8	8	10	4	0	0	0	7	D0				181	15	40
18	33	67	57	44	30	31	25	28	15	21	27	15	16	10	D3				422	15	4
19	14	73	57	33	28	18	22	15	11	10	4	5	0	D0					290	14	—
																		Means	300	14·6	—

D = died.

TABLE III.

Oviposition, etc., in moths not given sugar-water

No. of ♀	Days from commencement of experiment								Total eggs laid	Length of life in days	Approximate no. of mature eggs left in ovaries
	1	2	3	4	5	6	7	8			
	No. of eggs per day										
1 . .	75	44	41	D6					166	4	10
2 . .	84	57	28	3	D0				172	5	0
3 . .	35	77	110	59	8	6	2	D0	297	8	0
4 . .	72	30	7	D0					109	4	3
5 . .	59	50	16	0	0	0	D0		125	7	0
Totals per day .	325	258	202	68	8	6	2	0	Means		
									172	5·6	

D = died.

empty, of mature eggs, whereas there are no records of ovaries quite empty of mature eggs in Table II. This suggests that the starved moths laid all the mature eggs that were in the ovaries when they mated, but were unable to develop any of the immature ones, whilst those given sugar-water were able to do so. There is no doubt that this was so, for comparison of the appearance of the ovaries after death in the moths given sugar-water, with the ovaries of a virgin female, showed that the upper part of the ovaries which contains immature eggs was much larger in the virgin female than in those given sugar-water, especially those which had laid 400 or more eggs. It follows from the above that presumably the mean number of mature eggs in the ovaries at the time of mating is approximately that laid by the starved females, namely 172. Unfortunately this was not checked by dissection as there were no more virgin females available when the idea occurred to me. The potential number of eggs in the ovaries of a freshly mated female that was dissected was estimated at about 500. It may be remarked here that each ovary is composed of 4 ovarioles, each containing mature eggs in the lower third and increasingly immature eggs as one passes along the upper two-thirds; each ovary is bent twice on itself and thus divided into three parts.

It will be seen from Table II that on the whole the moths which laid the fewest eggs had the largest number of mature eggs remaining in the ovaries at death, and *vice versa.* If it is assumed that these mature eggs remaining in the ovaries would have been laid had the moth lived longer, one can say that the potential egg number was less variable than the actual number laid; this varied from 139 to 482 with a mean of 300. Five moths laid 400 or more eggs and it is probable that under the most favourable conditions the mean egg number would be nearer 400 than 300.

If the records for each moth in Table II are examined, it will be seen that the highest number of eggs laid in any one day was almost always during the first to fifth days of oviposition, regardless of when oviposition commenced; the mean falls at 3·4 days. With the starved females 4 out of 5 laid the highest number of eggs on the first day of oviposition and the mean is at 1·4 days; the total eggs per day shows a steady fall from a maximum value on the first day. If the corresponding daily totals are obtained from Table II, summing the values for the first, second, third days, etc., of oviposition, irrespective of when oviposition commenced, the nodal value falls on the third day instead of on the first, and the following figures are obtained: 483, 740, 879, 590, 659, 655, 421, 339, 248, 167, 193, 145, 92, 88, 50, 19, 7.

Of the total number of females employed in the egg-number experiments in which sugar-water was given, 8 proved to be unfertilised. The average length of life of these unfertilised females was the same as that of the fertilised ones (14·5 days), but the variability was a little greater; the shortest time being 10 days as against 11 in the fertile females, and the longest time 19 days as against 18. All the unfertilised females laid a few eggs, the lowest number being 9 and the highest 201 with a mean of 59. None of these eggs developed.

Some of the fresh males with which the females in the oviposition experiments were mated were also put separately in tubes with blotting-paper and sugar-water to see how long they would live. In order to be able to distinguish them from the older males after mating, a piece was clipped from the fore-wing of each of the fresh males before they were put in the box to mate. Thirteen males treated in this manner lived from 10 to 18 days, the mean length of life being 14·3 days.

As it had been noted that males put in with females on two or more nights seemed to die rather rapidly, an experiment was made to see whether males could mate more than once. Twelve fresh females were put in the box with six males that had emerged the day before and had already had one opportunity to mate. Eleven females were recovered and of these 5 were fertilised and 6 were not; the bursae in 4 of the 5 contained only small spermatophores. Evidently the males can mate on two successive nights, but apparently do not mate more than once in a night; so far as can be ascertained in none of the matings carried out was the number of females fertilised greater than the number of males present.

Eggs and first stage larvae.

The eggs are soft somewhat irregular-shaped objects, roughly oval in outline, about 0·5 mm. long, pressed flat against the surface on which they are laid, and only moderately convex in profile. They may be laid in close groups of 50 or more, sometimes two layers deep; or singly. The moth usually covers them with a few scales from the end of the abdomen and with any other dust lying about, each egg having one or two threads of blotting-paper and some scales adhering to it. A moth that was observed ovipositing was seen to press the tip of the ovipositor against the blotting-paper while the egg was extruded, at the same time rapidly vibrating the last segments of the abdomen up and down; it seems probable that in this way the stout brush at the end of the abdomen was enabled to draw up a few strands of the blotting-paper over the newly laid egg.

When laid the eggs are a creamy buff in colour and smooth, but the appearance alters considerably with age. The colour darkens from buff through orange to orange-pink, attaining the maximum depth of colour by about the 6th day. The pink colour is dorsal and is not present on the underside of the egg or around the attached margin. At about the 6th day faint longitudinal furrows may appear on the egg and these may later develop into a network of acute ridges upon the egg; not all the eggs display these ridges, which are no doubt an effect of shrinkage. By the 13th day the ocelli of the embryo larva are just beginning to be visible and by the 16th day they are well developed as a pair of round black spots, and the pigmentation of the whole head and of the prothoracic plate is just becoming visible. Shortly before hatching the larva is plainly visible through the transparent chorion of the egg, lying curled up head to tail. The eggs hatched in 18 to 21 days, the majority on the 19th day; about 95% hatched. This was in the laboratory at a temperature of 17–21° C.

The larvae are about 1·0 mm. long and orange-yellow with a black head and prothoracic plate. The anal plate is the same colour as the body. Down the middle of the body in newly hatched larvae runs an orange-pink line which is evidently due to the presence in the gut of the orange substance from the egg; this darker line is not present in older larvae and the substance is evidently absorbed or voided.

A few hours after hatching the larvae begin to search for suitable places in which to hibernate until the following spring. They are strongly thigmotropic, and creeping into the smallest spaces possible they spin around themselves a small silken cocoon. Spinning up is completed in from 24 to 48 hours after hatching and apparently no food is taken in this time; a piece of *Heracleum* offered was left untouched.

NOTE BY O. W. RICHARDS.

After Mr. J. A. Reid had left for Malaya, the young larvae were hibernated in the tubes in an open summerhouse. They were brought indoors for examination at the end of March and in early April. The larvae then very rapidly left their hibernation cocoons and began wandering. Mr. J. A. Downes tried to get them to feed, using every device we could think of, but nearly all refused everything offered. A few seemed to make the beginning of a small mine, but this was not continued. All the several thousand larvae died in a week or two.

NOTES ON THE FOOD OF *MICROPEPLUS*, WITH A DESCRIPTION OF THE PUPA OF *M. FULVUS* ERICHSON (COLEOPTERA, MICROPEPLIDAE)

By H. E. Hinton, Ph.D., and F. L. Stephens, M.Sc.

(*British Museum* (*Natural History*).)

The family Micropeplidae contains only two genera, *Kalissus* Lec. with one species in western North America and *Micropeplus* Latr. with 24 species widely distributed in the holarctic region and one in Central America. Nothing has been recorded of the food of these beetles and the only description of their immature stages is that of Lubbock (1868) of the larva of *M. staphylinoides* Marsham (1802) which he found on the underside of dead boughs. According to Thomson (1862) the adults live almost exclusively in mud by the side of lakes and streams. Fowler (1889) recorded them in haystack and vegetable refuse and Ganglbauer (1899) under decaying vegetation, in mouldy wood, and in dung.

Nature of the Food.

While collecting (12.i.1941) in a compost heap [1] in the grounds of Linton Village College, Cambridgeshire, five larvae, one pupa, and four adults of *M. fulvus* Erichson (1840) were taken. The adults and larvae were found about two feet from the top of the heap on or near the ground among very decayed and partly liquefied cabbage leaves and other plant refuse. The pupa was found in a small cell about an inch below the surface of the ground at the bottom of the compost heap.

To discover the food of the beetle, the following experiments were made. One adult was placed in a petri dish lined with moist filter paper and containing barley flour, preserved fig, bread, coffee, chocolate, and two common fungi, the common green mould ("*Penicillium glaucum*") and the cultivated mushroom (*Psaliota campestris*). Next day the beetle was removed to a clean slide and its pellets collected. These contained some starch grains from the barley and *Penicillium* conidia. Faeces found in the petri dish were of similar composition. On the third day the beetle was dead, having become entangled in deliquescent chocolate.

The above experiment was repeated using two recently emerged adults (still pale brown in colour) and one mature adult. After the first day the faeces of the two immature beetles consisted of a mixture of *Penicillium* conidia, *Psaliota* spores, and some starch and coffee. In these faeces the mushroom spores predominated. The pellets of the mature specimen consisted entirely of *Penicillium* conidia. The excrement of these beetles was examined daily for a week, and those of the mature beetle consisted almost entirely of *Penicillium* conidia, while those of the less mature specimens consisted of a mixture of the two fungi. One of these specimens, the most mature, was later fed on dry rot fungus (*Merulius lacrymans*), which it ate readily.

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[1] This heap more or less fills a pit in the ground about ten feet square and three feet deep. This pit, according to the gardener, Mr. Jacob, has been used to decompose plant refuse for nearly two years. During the warmer parts of the year it is swarming with beetles, Staphylinidae, Trichopterygidae, Hydrophilidae (*Cercyon*), and Cryptophagidae (*Atomaria*, *Ephistemus*) being particularly numerous in individuals. In mid-winter the beetle population is notably reduced, the Trichopterygidae, Hydrophilidae, and Cryptophagidae being absent or rare and the common summer Staphylinidae being replaced by a few mid-winter species such as *Quedius cinctus* Paykull (1790) and *Tachinus subterraneus* Linnaeus (1758). Larvae, pupae, and adults of *Q. cinctus* were rather abundant as were also larvae and adults of *T. subterraneus*.

The *Penicillium* conidia in the excrement are at least partly digested. A microscopic examination shows that a proportion of the conidia have collapsed, while in others the walls are thin or even broken so that they have a crescent shape. When the pellets were kept in water at room temperature (65° F. ± 5°) approximately 15% of the conidia became swollen and put out germ tubes on the second and third days. *Penicillium* conidia taken from the same culture, but which had not been ingested by the beetles, did not germinate until the eighth day. This seems to show that, in the case of the 15% or so of the spores that survive ingestion, the time taken for germination is considerably decreased by passage through the alimentary canal of *Micropeplus*. A possible explanation of this phenomenon may be that in a small number of spores (about 15%) the walls are thinned by the enzymes [2] of the beetle but not killed, so that they are rendered more susceptible to external physical conditions, *e.g.* moisture. *Psaliota* spores that pass through the alimentary canal are also often broken.

To discover if *Micropeplus* will transmit fungi externally, two specimens were placed in a tube containing sterile medium. Two days later the tracks of their footsteps showing where they had walked were represented by small colonies of *Penicillium*.

In a wood near Linton one larva and five adults of *M. staphylinoides* were found (26.i.1941) on the underside of several specimens of *Polyporus squamosus*. Faeces of these were examined, and in both larvae and adults were found to contain bacteria, fungal hyphae, and the spores of the following fungi: *Penicillium* sp., *Cladosporium herbarum*, *Fumago vagans*, *Botrytis cinerea*, and hyaline spores possibly belonging to a Basidiomycete.

The two species do not appear to be carnivorous in either the larval or adult stages. The five larvae and four adults of *M. fulvus* were kept for 24 hours in a tube containing a few small Dipterous larvae, and at the end of this time showed no signs of having attacked each other or the Diptera. The single larva and five adults of *M. staphylinoides* were also kept for nearly 24 hours in a tube containing two Dipterous larvae, one small Staphylinid larva, and two specimens of the small Lathridiid, *Coninomus nodifer* Westwood (1839). At the end of this time they had apparently not attacked each other or the other species with them.

DESCRIPTION OF THE PUPA (figs. 1–3).

Female: Length, 1·9 mm.; breadth (across broadest point of abdomen), 0·9 mm. Body obovate, moderately depressed. Cuticle white and clothed only with a number of erect, moderately long and stout setae (fig. 1). *Head* not visible from above or at most with eyes and part of vertex visible. Front moderately concave and eyes very prominent.

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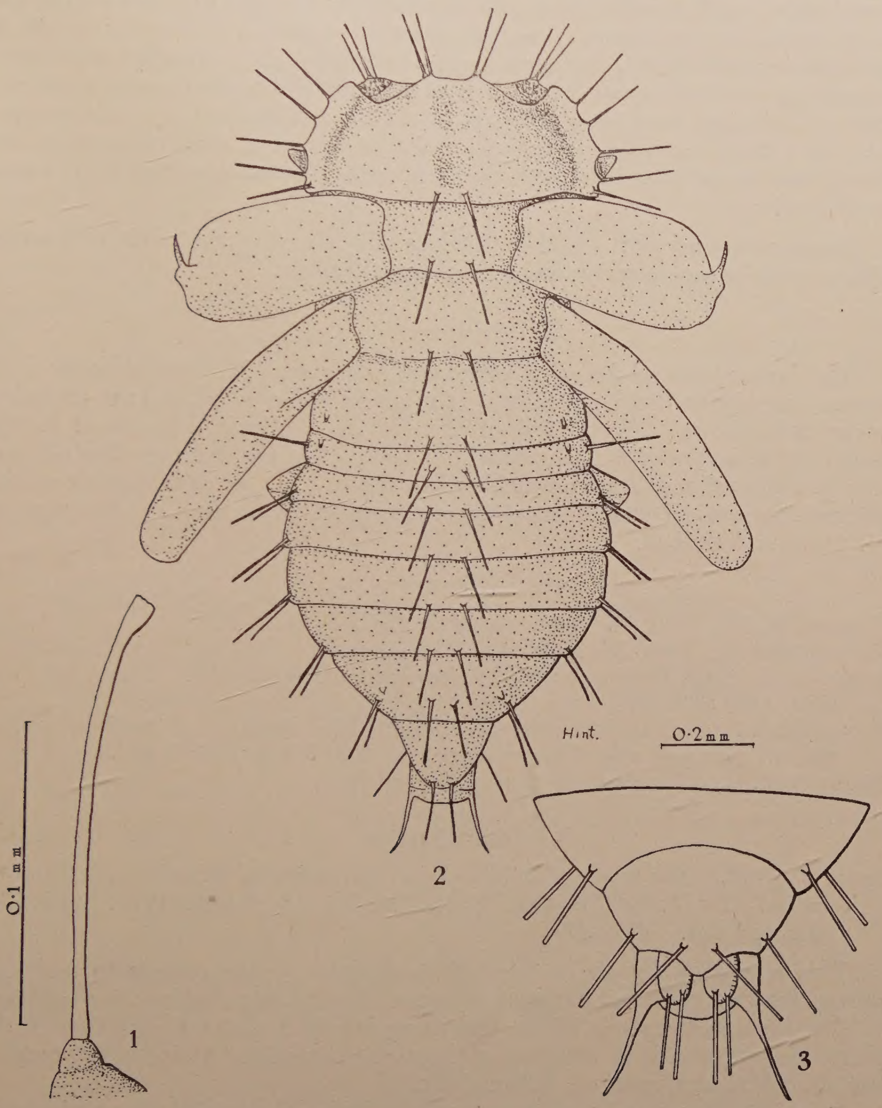
[2] Cellulase has been recorded in a number of wood-eating beetles (Mansour and Mansour-Bek, 1934). It is also possible that the "fungus cellulose" of the walls of the conidia may be fermented by bacteria in some part of the gut, as has been shown to be the case in the larvae of some beetles (e.g. *Cetonia*) and in the wood-feeding cockroach, *Panesthia*.

Surface glabrous except for three long setae which arise from near middle top of eye. Antennae extending to posterior third or fourth of prothorax in a deep, concave area on ventral side. *Pronotum* with shape and impressions as shown in fig. 2; with eight setae on each side as follows: two near middle of anterior margin; four more or less evenly spaced on lateral margin; and two near basal margin, one near middle and one very near basal angle. Mesonotum without distinct impressions and with a single seta on each side of middle near posterior margin; elytra extending postero-laterally to about basal half of first abdominal tergite and on middle apical margin with a long, thick spine which is directed forwards and lies on the same plane as elytra. Metanotum without distinct



Figs. 1–3.—Pupa of *Micropeplus fulvus* Erichson. 1. Pronotal seta. All setae when enlarged are similar in shape. 2. Dorsal view of pupa. Wings were partly extended in Pampel's fluid. 3. Ventral view of apex of abdomen of female.

impressions and with a single seta on each side of middle near posterior margin; wings extending posteriorly and ventrally to posterior margin of fourth abdominal sternite. Abdomen with first tergite very long and with a single seta on each side of middle near posterior margin; second tergite on each side with a seta near middle of lateral margin and one near middle half-way between anterior and posterior margin; third to seventh tergites setose like second but with lateral seta nearer posterior margin; eighth tergite nearly as long as broad, apical margin strongly rounded, and with a single seta on each side of middle; ninth tergite with each postero-lateral angle produced to form a long seta-like process. Abdominal sternites one to five with a single seta on each side near postero-lateral angle; sixth sternite (fig. 3) similarly setose and also with a seta on each side of middle near posterior margin. *Legs* with front pair extending to anterior margin of metasternum; tarsi separated by a distance equal to length of tibia. Middle pair extending to posterior two-thirds of metasternum; tarsi as widely separated as those of front pair. Hind pair extending to posterior margin of third abdominal sternite; apex of tarsi separated by a distance equal to their own length. Abdominal spiracles dorso-lateral and those of the first and second segments opening in apices of short, cylindrical, feebly sclerotised tubercles.

Specimen examined: 1 ♀, identified as *M. fulvus* by the adult characters which could be seen clearly through the pupal cuticle.

SUMMARY.

The larvae and adults of *Micropeplus fulvus* and *M. staphylinoides* feed almost entirely on fungi, particularly the spores and conidia, and are probably never carnivorous. About 15% of the conidia of *Penicillium* found in the faeces of the adults of *M. fulvus* had not been killed but were so affected that they germinated much more quickly than usual. *M. fulvus* is capable of the internal mechanical and external transmission of *Penicillium*. The pupa of *M. fulvus* is described.

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Coconut Quest. The story of a search in the Solomon Islands and the East Indies. By J. S. PHILIPS. 8vo. London (Jarrolds), 1940. pp. 254, 30 pls., 4 figs. Price 16*s*.

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